Heritability of phenotypic udder traits to improve resilience to mastitis in Texel ewes

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Short title: Heritable traits against mastitis in suckler ewes

Abstract

There are no estimates of the heritability of phenotypic udder traits in suckler sheep, which produce meat lambs, and whether these are associated with resilience to mastitis. Mastitis is a common disease which damages the mammary gland and reduces productivity. The aims of this study were to investigate, the feasibility of collecting udder phenotypes, their heritability and

their association with mastitis in suckler ewes. Udder and teat conformation, teat lesions, intramammary masses (**IMM**) and litter size were recorded from 10 Texel flocks in Great Britain between 2012 and 2014; 968 records were collected. Pedigree data were obtained from an online pedigree recording system. Univariate quantitative genetic parameters were estimated using animal and sire models. Linear mixed models were used to analyse continuous traits and generalised linear mixed models were used to analyse binary traits. Continuous traits had higher heritabilities than binary with teat placement and teat length heritability (h^2) highest at 0.35 (s.d. 0.04) and 0.42 (s.d. 0.04) respectively. Udder width, drop and separation heritabilities were lower and varied with udder volume. The heritabilities of IMM and teat lesions (sire model) were 0.18 (s.d. 0.12) and 0.17 (s.d. 0.11) respectively. All heritabilities were sufficiently high to be in a selection programme to increase resilience to mastitis in the population of Texel sheep. Further studies are required to investigate genetic relationships between traits and to determine whether udder traits predict IMM, and the potential benefits from including traits in a selection programme to increase resilience to chronic mastitis.

Keywords: genetics; intramammary infection; meat sheep; pedigree; selection

Implications

In the UK, mastitis is a very common cause of early culling and reduced production in suckler sheep, with 30% of ewes with intramammary masses and 8% of ewes culled for mastitis each year. Currently, there is no strategy to reduce the occurrence of mastitis in pedigree suckler sheep. The results from

the current study suggest that it might be possible to improve resilience to mastitis in Texel sheep and, by analogy, other meat producing pedigree breeds of sheep, through selection of desirable phenotypic udder traits.

Introduction

There are 18 million breeding ewes in the UK. Most ewes suckle lambs either for meat production or replacement stock; dairy sheep flocks producing milk are rare. Mastitis is one of the most prevalent and costly endemic diseases in suckler ewes. Farmers have estimated that acute mastitis occurs in 0-5% of suckler ewes per annum (Cooper *et al.,* 2016), however, this is probably an under-estimate because mastitis is typically detected when it is chronic, as intramammary masses (**IMM**) that are typically abscesses that contain a range of bacterial species, although Staphylococcal species dominate (Smith *et al.*, 2015). Intramammary masses are strongly associated with an increased risk of acute mastitis and IMM also result from acute mastitis (Grant *et al.*, 2016). Detection of IMM occurs when udders are palpated at weaning or prior to mating and, in a recent study, approximately 30% of ewes had an IMM (Grant *et al.,* 2016). They cause reduction in milk production and consequently reduced lamb growth rates (Huntley *et al.,* 2011). It is possible that approximately 8% of the national flock is culled each year because of mastitis (Cooper *et al.,* 2016). There is no estimate of the cost of mastitis to the commercial sheep industry in the UK, however, using parallels with dairy cattle, Conington *et al.,* (2008), estimated that mastitis cost the UK Texel sheep breed of approximately 100,000 ewes £2.7 million per annum.

The majority of studies of heritability of mastitis in sheep have been done in dairy ewes (e.g. Casu *et al.*, 2010, de la Fuenta *et al.,* 2011, Fernandez *et al*., 1997, Legarra and Ugarte, 2005, Makovický *et al*., 2015), where udder and teat traits were heritable and genetically correlated with somatic cell count (**SCC**) or somatic cell score. In crossbred suckler ewes, udder and teat phenotype are

associated with raised SCC, indicative of subclinical mastitis (Huntley *et al.*, 2012), and traumatic teat lesions (Cooper *et al.*, 2013).

It is likely that udder conformation in Texel ewes is heritable, as it is in dairy sheep, however, there is a dearth of information on the heritability of traits associated with mastitis in any breed of suckler ewes (Conington *et al.*, 2008). Anecdotally, farmers comment that acute mastitis and IMM are also common in pedigree suckler sheep. In a recent on-farm study the farmer-recorded rate of acute clinical mastitis in four Texel flocks was 2-42 cases / 100 ewes p.a. and the percentage of ewes with IMM at whole flock inspections ranged from 8% - 43% (Grant *et al.*, 2016). In that study, the prevalence of IMM was higher in pedigree flocks than commercial flocks, possibly because lambs born to high genetic merit ewes with IMM or non-functioning glands are not culled because lambs can be reared by surrogate ewes.

The hypothesis for the current study was that suckler ewe resilience to mastitis could be improved through selective breeding of heritable traits associated with chronic mastitis to reduce its occurrence and that of acute mastitis. The aim of this paper was to investigate the feasibility of collecting observations of udder phenotype and IMM to assess whether udder and teat traits are heritable in Texel sheep.

Material and Methods

Selection of flocks and ewes and data collection

Ten pedigree Texel flocks, with individual ewe identification and which performance-recorded using the Beef and Sheep Company database (**BASCO**) database, were convenience selected based on recommendation and farmer

interest in participating in the study. The flocks were located in England, Scotland and Wales. All Texel ewes in each flock were included in the study, which took place between 2012 and 2014. Each flock was visited on one occasion each year; eight flocks were visited once, one twice and one three times depending on farmer compliance and when they joined the study. Ewes lambed between January and May and data collection occurred in mid-lactation with the majority of ewes 7 – 14 weeks into lactation (Table 1). All measurements were performed by two authors (EMS and CG) and data were recorded into a custom-designed data logger. Four flocks contributed data to Grant *et al*., (2016) and these flocks also recorded acute mastitis, however the other six Texel flocks did not record acute mastitis.

Data collected on udder and teat traits

Linear scores with nine categories were used to characterise teat angle, udder depth, and the degree of separation of udder halves as described previously (Marie-Etancelin *et al.*, 2005, Casu *et al.*, 2006, Grant *et al.*, 2016). A tape measure was used to record udder width at the widest point as viewed from the rear. Only the left teat length was recorded because there was a very strong positive correlation between left and right teat length and width (Smith, unpublished data). Palpable masses in the udder were defined as IMM and recorded as present or absent. Teat lesions were defined as any lesion present on the teat including bites, tears, grazes, spots, warts and proliferative scabs (Cooper *et al.*, 2013) and were also recorded as present or absent.

Data preparation

Data collected on farms were entered into Microsoft Excel spreadsheets. Ewe age in years at the time of observation was calculated as the difference between birth date and data collection date, and number of days in milk (**DIM**) was calculated as the difference between lambing date and data collection date. Traits recorded on a continuous scale, or with nine categories, were treated as normally distributed (Table 2). Teat lesions and IMM were considered as binary data (Table 3). The principal fixed effects were flock-score observation date (**FSD**) which included the effect of the flock and scorer on that day, ewe age (**EA**) in years (2, 3, 4, 5 and >5), and a linear regression of DIM. Litter size was coded into single or multiple births and 'observed on farm' or sourced from 'BASCO-derived' data (Table 4). Both estimates were prone to error because the former might have had fostered lambs recorded to their foster ewe and the latter because farmers only enter lambs into BASCO that they intend to monitor. Litter size was included in the fixed effect model for some analyses. Records from one-year old ewes and those with no observation date, lambing date or unknown sire were removed. This left 817 udder trait records from 740 ewes; 665, 73 and 2 with one, two or three observations respectively.

Pedigree records from the BASCO database were concatenated to provide a pedigree file for the 740 ewes. The pedigree was pruned to remove uninformative members leaving 2270 sheep in the pedigree that were included in the animal model analyses (see below). There were 188 sires and maternal grandsires that were used to create the sire-maternal grandsire relationship matrix for the sire models. The 740 ewes were the offspring of 145 sires with an

average of 5.6 ewe records / sire; there were 39 rams with only one recorded ewe offspring in the dataset.

Data analysis

Three datasets were used; all 817 records which included repeated observations on some ewes, 740 single records per ewe using the last observation for each ewe, and 713 records with information on litter size (a subset of the 740 single ewe record data set). Univariate quantitative genetic analyses were performed using individual animal models (**IAM**) for continuous traits and both IAM and sire models for binary traits. Bayesian Integrated Nested Laplace Approximation (**INLA**) (Rue *et al.*, 2009) in the inla R package (http://r-inla.org) was used for all genetic analyses, the fitting of IAM with INLA having been demonstrated previously by Holand *et al.* (2013). The fixed effects model (with FSD only or FSD plus EA or DIM or both) which resulted in the lowest deviance information criterion (Spiegelhalter *et al.*, 2002) was used in the reported analyses for that trait.

The following individual animal models were considered:

$$\mathbf{y = Xb + Za + e} \qquad (1)$$

$$\mathbf{y = Xb + Za + Zu + e} \qquad (2)$$

Where: **y** is a vector of phenotypic observations; **b** is a vector of fixed effects; **a** is a vector of random animal effects; **u** is a vector of random permanent environmental effects associated with ewes; **X** and **Z** are design matrices relating observations to fixed effect levels or animals, respectively; and **e** is a vector of random residual effects. The variance of **a** is $var(\mathbf{a}) = \mathbf{A}\sigma_a^2$, where **A**

is the numerator relationship matrix, the variance of **u** is $var(\mathbf{u}) = \mathbf{I}\sigma_{pe}^2$ and the variance of **e** is $var(\mathbf{e}) = \mathbf{I}\sigma_e^2$.

There is evidence that sire models provide better estimates of variance components than animal models for binary traits (Ødegård *et al.,* 2010). Consequently, a sire model with relationships was considered for the binary traits.

The following sire model was used:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Zs} + \mathbf{e} \qquad (3)$$

Where: **y** is a vector of phenotypic observations; **b** is a vector of fixed effects; **s** is a vector of random sire effects; **X** and **Z** are design matrices relating observations to fixed effect levels or sires, respectively; and **e** is a vector of random residual effects. The variance of **s** is $var(\mathbf{s}) = \mathbf{A_s}\sigma_s^2 (\sigma_s^2 = 0.25\sigma_a^2)$, where $\mathbf{A_s}$ is the sire-maternal grandsire numerator relationship matrix pertaining to the 188 animal sire-maternal grandsire pedigree. A binomial GLMM with logit link function was fitted, therefore with a fixed residual variance, $\sigma_e^2 = \frac{\pi^2}{3}$.

The same prior probability distribution was assumed for the heritability of all traits: a beta distribution with a mode of 0.15 and in which 95% of the distribution fell below a heritability of 0.7. To obtain priors for genetic and residual precisions of continuous traits, random samples were taken from the prior distribution for heritability, which were converted to precisions assuming a phenotypic variance of 1, and a gamma distribution was fitted to the resulting samples. To obtain trait-specific priors, the rate parameters of the fitted gamma distributions were scaled by an approximation of the phenotypic variance for each trait. For the sire model of binary traits, the sire effect precision must be $\tau_s \geq \frac{9}{\pi^2}$. The R

'logspline' procedure (Kooperberg, 2013) was used to approximate the prior distribution taking account of this truncation. Priors for models incorporating repeated observations of ewes were determined by extending the method above to include the precision of ewe permanent environment effects. The power of the dataset to estimate genetic correlations was limited, because of its small size and many sires with < 5 offspring, and so Pearson's correlations between the maximum a posteriori (**MAP**) estimated breeding value (**EBV**) of the 45 sires with more than 5 ewe offspring in the dataset were used as a robust subset to investigate genetic correlations between traits.

Results

Descriptive analyses

The following summary statistics contextualise the data used in the model and the types of flocks and sheep studied. The number of recorded ewes per flock ranged from 32-152. The median data collection was done ten weeks into lactation, range 1-18 weeks. Two- and three-year-old ewes were most frequently observed. The average litter size for researcher-recorded records was 1.59 lambs per ewe, and for records obtained through BASCO 1.66 lambs per ewe (Table 4). There were 224/740 (30%) ewes with an IMM and 139 (20%) ewes with one or more teat lesion (Table 3). Teat placement and udder depth were normally distributed whereas degree of separation was positively skewed and udder width was negatively skewed (Table 2).

Multivariable models of heritability

The combination of fixed effects with the lowest deviance information criterion (**DIC**) value was used for each trait modelled in all analyses (Supplementary Table S1). For Teat Placement and Udder Width the selected fixed effect model included FSD, EA and DIM. For Udder Depth DIM was omitted while EA was omitted for the Left Teat Length model. For the binary traits and Degree of Separation, FSD was the only fixed effect included. Teat placement and teat length heritabilies (h^2) were = 0.35 (s.d. 0.04) and 0.42 (s.d. 0.04) respectively. Udder width, drop and separation heritabilities were lower than this and varied with udder volume. The continuous udder traits MAP estimates ranged from 0.10 (for udder width) to 0.42 (left teat length) (Table 5). Heritability estimates for the binary traits were lower than the continuous traits, the heritability of IMM and teat lesions in the sire model was 0.18 (s.d. 0.12) and 0.17 (s.d. 0.11) respectively. The sire model MAP estimates (Table 6) were higher than those from the animal model (Table 7) for three out of four traits. All heritabilities were sufficiently high that they could be used in a selection programme to increase resilience to mastitis in the population of Texel sheep, they were generally slightly higher when repeated scores were included (Supplementary Table S2). Non-zero estimates of the permanent environmental variance were obtained for udder depth, degree of separation and udder width (Supplementary Tables S2 and S3), indicating that these variables varied by flock. The modal heritability was generally slightly lower when litter size was included in the model, except for teat placement and chronic mastitis (Supplementary Tables S4 and S5). The mode and 95% credible intervals for the chosen prior were similar to those obtained when a uniform prior for the heritability was used. For the continuous traits (Supplementary Figure S2), the credible interval of the heritability was

reasonably consistent across priors. For the binary traits (Supplementary Figure S3) the 95% credible interval varied with the width of the prior distribution. The estimates of Pearson's correlations between MAP estimates of EBV of sires with at least 5 recorded ewe offspring indicated that non-zero genetic correlations may exist between the traits (Supplementary Table S6).

Discussion

This is the first study to investigate the heritability of udder traits in pedigree suckler ewes. The continuous udder traits were heritable (Table 5), as in studies of dairy sheep (de la Fuenta *et al.,* 2011, Fernandez *et al.,* 1997, Makovický *et al*., 2015). However, because udder width and degree of separation are influenced by udder fullness, their inclusion in a selection programme would require care, taking account of any relationships with, for example, maternal effects on lamb growth. The heritability of binary traits such as teat lesions and IMM (Table 6) was lower than continuous traits and consequently direct selection for these traits would progress more slowly than for the continuous traits. The difference in heritability of teat lesions (Table 6) highlights the influence of random error in our small dataset, a future study would require more observations on binary traits to reduce random error. Overall, the phenotypic trait estimates of heritability were similar to those reported in several breeds of dairy sheep (de la Fuenta *et al.,* 2011, Fernandez *et al.,* 1997, Makovický *et al.,* 2015) and, with large standard deviations observed, any differences in heritability estimates are likely to be non-significant. It is therefore likely that udder traits would be heritable in other pedigree suckler breeds of sheep.

Several approaches to the analysis of the data were taken in an attempt to maximise the confidence in the results from the relatively small dataset. The heritability of binary traits was slightly higher in the sire model (Table 6) than the animal model (Table 7), with the posterior distributions more skewed towards higher values but with posterior modes that were similar to those from the animal model. Previous literature indicates that the sire model estimates of heritability for binary traits may be better estimates of the true h^2 than individual animal model estimates, see Ødegård *et al.,* (2010) for a discussion and a proposed solution for estimation of genetic parameters using Markov chain Monte Carlo.

The dataset was too small to perform multivariate quantitative genetic analysis to investigate the genetic relationships of udder traits to resilience to IMM. Measuring indirect traits might be a route to improve resilience to IMM should traits be correlated with IMM as suggested by our crude analysis (Supplementary Table S6) and previously in suckler ewes (Huntley *et al.*, 2012) and dairy ewes (Casu *et al.,* 2010, Legarra and Ugarte, 2005). If udder traits are not linked to IMM selection for resilience to IMM would have to be done through direct observation and recording of IMM.

We focused on the Texel breed because farmers were compliant with the study and the flocks in our study had good pedigree information stored electronically in the (BASCO). It is important to consider that it would only be cost-effective to initiate a programme to record such data if the prevalence of undesirable phenotypes in Texel ewes was sufficiently high to make such selection useful. The prevalence of poor udder and teat conformation was low in Grant *et al.* (2016) where several breeds and crossbreeds were studied. Consequently, the

prevalence of undesirable phenotypes in Texel ewes needs to be established from a random sample of Texel flocks before a selection programme is started. Covariates that influenced the estimates and precision of heritabilities included ewe age, DIM and litter size whether using the observed or BASCO recorded estimates. These data are collected routinely in BASCO and could be included in future analyses. There was also evidence that repeated observations of traits the same ewe across years increased the precision of estimates of heritability for some traits. So, ideally a ewe's phenotype should be measured several times over her life. This adds to the challenge of collecting phenotypic trait data because the time spent recording udder phenotype data would be considerable. In addition, farmers have been reluctant to record disease traits because they are disadvantageous to record unless all farmers recorded mastitis. A strategy to collect robust data would be required so that all flocks are recorded to a good standard and farmers can make informed choices on the genetic merit of sheep with regard to resilience to IMM.

In conclusion, results from this study of 740 Texel ewes indicate that udder traits were heritable although binary traits had lower heritability, with less precision, than continuous traits. These are new and useful results. The next stages are to use a larger dataset to perform multivariate analysis to estimate the genetic relationships between udder traits and of udder traits with IMM and to estimate the proportion of Texel ewes with poor udder conformation before a programme to improve resilience to mastitis through selection is implemented. Finally, a robust selection programme would require repeated observations of ewes within a flock and for many, preferably all, BASCO recorded Texel flocks to record mastitis traits.

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Declaration of interest

There are no conflicts of interest to declare.

Ethics statement

This study was approved by the University of Warwick biomedical and scientific research ethics committee.

Software and data repository resources

There is no software from this study. None of the data were deposited in an official repository.

References

Casu S, Pernazza I and Carta A 2006. Feasibility of a linear scoring method of udder morphology for the selection scheme of Sardinian sheep. Journal of Dairy Science 89, 2200-2209.

Casu S, Pernazza I and Carta A 2010. Phenotypic and genetic relationships between udder morphology and udder health in dairy ewes. Small Ruminant Research 88, 77-83.

Conington J, Cao G, Stott A and Bünger L 2008. Breeding for resistance to mastitis in United Kingdom sheep, a review and economic appraisal. The Veterinary Record 162, 369-376.

Cooper S, Huntley SJ and Green LE 2013. A longitudinal study of risk factors for teat lesions in 67 suckler ewes in a single flock in England. Preventive Veterinary Medicine 110, 232-241.

Cooper S, Huntley SJ Crump R, Lovatt F and Green LE 2016. A cross-sectional study of 329 farms in England to identify risk factors for ovine clinical mastitis. Preventive Veterinary Medicine 125 89 - 98.

de la Fuente LF, Gonzalo C, Sànchez J, Rodríguez R, Carriedo J and Primitivo F 2011. Genetic parameters of the linear body conformation traits and genetic correlations with udder traits, milk yield and composition, and somatic cell count in dairy ewes. Canadian Journal of Animal Science 91, 585-591.

Fernandez G, Alvarez P, San Primitivo F and de la Fuente LF 1995. Factors affecting variation of udder traits of dairy ewes. Journal of Dairy Science 78, 842-849.

Grant C, Smith EM and Green LE 2016. A longitudinal study of factors associated with acute and chronic mastitis and their impact on lamb growth rate in 10 suckler sheep flocks in Great Britain. Preventive Veterinary Medicine 127, 27-36.

Holand AM, Steinsland I, Martino S, and Jensen H 2013. Animal models and integrated nested Laplace approximations. Genes, Genomes, Genetics 3, 1241 – 1251.

Huntley SJ, Cooper S, Bradley AJ and Green LE 2012. A cohort study of the associations between udder conformation, milk somatic cell count, and lamb weight in suckler ewes. Journal of Dairy Science 95, 5001-5010.

Kooperberg C 2013. logspline: Logspline density estimation routines. R package version 2.1.5. Accessed on 02nd October 2018 from https://cran.r-project.org.

Legarra A and Ugarte A 2005. Genetic parameters of udder traits, somatic cell score, and milk yield in Laxta sheep Journal of Dairy Science 88, 2238-2245.

Makovický P, Margetín M, Makovický P, 2015. Genetic parameters for the linear udder traits of nine dairy ewes. Veterinarski Arhiv 85, 577-582.

Marie-Etancelin C, Astruc JM, Porte D, Larroque H and Robert-Granié C 2005. Multiple-trait genetic parameters and genetic evaluation of udder-type traits in Lacaune dairy ewes. Livestock Production Science 97, 211-218.

Ødegard J, Meuwissen TH, Heringstad B and Madsen P 2010. A simple algorithm to estimate genetic variance in an animal threshold model using Bayesian inference. Genetics Selection Evolution 42, 29.

Rue H, Martino S and Chopin N 2009. Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. Journal of the Royal Statistical Society 71, 319-392.

Smith EM, Willis ZN, Blakeley M, Lovatt F, Purdy KJ and Green LE 2015. Bacterial species and their associations with acute and chronic mastitis in suckler ewes. Journal of Dairy Science 98, 7025-7033.

Spiegelhalter DJ, Best NG, Carlin BP and van der Linde A 2002. Bayesian measures of model complexity and fit. Journal of the Royal Statistical Society Series B 64, 583-639.

Table 1 *Number of observations by age and week of lactation for 740 ewes*

Ewe age in years	2	3	4	5	>5				
Number of observations	255	215	127	69	74				
Week of lactation	1-2	3-4	5-6	7-8	9-10	11-12	13-14	15-16	17-18
Number of observations	4	16	63	193	219	217	53	2	50

Table 2 *Summary statistics for continuous udder traits for 740 ewes*

Trait	Mean	SD	Mi	Score								
				1	2	3	4	5	6	7	8	9
Teat placement	5.87	1.16	4	0	4	10	60	204	243	159	51	5
Udder depth	6.93	0.86	4	0	0	2	7	18	179	348	174	8
Degree of separation	3.23	1.38	54	47	188	201	114	90	37	8	1	0
	Mean	SD	Mi	Minimum		Maximum						
Udder width cm	13.45	2.09	5	5.0		20.0						
Left teat Length cm	2.5	0.44	4	1.0		4.0						

Mi = missing, Score = trait linear score

Table 3 *Number and percentage of binary udder traits for 740 ewes*

	No	Yes	Percentage	Missing
Chronic mastitis	516	224	30	0
Left teat lesion	652	88	12	0
Right teat lesion	639	101	14	0
Any teat lesion	601	139	20	0

Table 4 *Litter size for 713 ewes from farmer records and the Beef and Sheep Company database (BASCO) database*

Source	Litter size	
	Single	Multiple
Farmer records	123	127
BASCO database	189	274

Table 5 *Marginal distributions of variance components and heritabilities of continuous udder traits of 740 ewes from an individual animal model Bayesian Integrated Nested Laplace Approximation analyses*

Trait	Parameter	Mean	SD	Percentiles			MAP
				2.5%	50%	97.5%	
Teat placement	σ_e^2 [1]	0.67	0.08	0.53	0.67	0.82	0.67
	σ_a^2 [2]	0.36	0.09	0.2	0.35	0.55	0.34
	h^2 [3]	0.35	0.04	0.27	0.35	0.43	0.35
Udder depth	σ_e^2	0.5	0.05	0.4	0.5	0.59	0.50
	σ_a^2	0.13	0.05	0.04	0.12	0.24	0.11
	h^2	0.21	0.04	0.13	0.21	0.3	0.21
Degree of separation	σ_e^2	1.32	0.15	1.05	1.31	1.6	1.32
	σ_a^2	0.47	0.16	0.21	0.45	0.81	0.42
	h^2	0.27	0.04	0.19	0.27	0.36	0.27
Udder width	σ_e^2	2.61	0.2	2.22	2.61	3	2.62
	σ_a^2	0.36	0.18	0.09	0.33	0.79	0.25
	h^2	0.12	0.04	0.05	0.11	0.2	0.10
Left teat length	σ_e^2	0.11	0.01	0.08	0.11	0.14	0.11
	σ_a^2	0.08	0.02	0.05	0.08	0.12	0.08
	h^2	0.42	0.04	0.35	0.42	0.5	0.42

MAP = maximum a posteriori probability

[1] σ_e^2 = variance of e = vector of random residual effects

[2] σ_a^2 = variance of a = vector of random animal effects

[3] h^2 = *heritability*

Table 6 *Marginal distributions of heritabilities from sire model Bayesian Integrated Nested Laplace Approximation analyses of binary udder traits of 740 ewes*

Trait	Parameter	Mean	SD	Percentiles			MAP
				2.5%	50%	97.5%	
Chronic mastitis	σ_e^2 [1]	0.16	0.11	0.02	0.14	0.43	0.10
	σ_a^2 [2]	0.65	0.44	0.07	0.56	1.71	0.39
	h^2 [3]	0.18	0.12	0.02	0.16	0.46	0.12
Left teat lesion	σ_e^2	0.12	0.08	0.01	0.11	0.29	0.03
	σ_a^2	0.49	0.33	0.03	0.44	1.16	0.13
	h^2	0.14	0.09	0.01	0.13	0.32	0.04
Right teat lesion	σ_e^2	0.23	0.17	0.02	0.2	0.67	0.11
	σ_a^2	0.94	0.69	0.07	0.79	2.7	0.45
	h^2	0.26	0.17	0.02	0.23	0.68	0.14
Any teat lesion	σ_e^2	0.15	0.1	0.01	0.13	0.35	0.04
	σ_a^2	0.6	0.41	0.04	0.51	1.42	0.16
	h^2	0.17	0.11	0.01	0.15	0.39	0.05

MAP = maximum a posteriori probability

[1] σ_e^2 = variance of e = vector of random residual effects

[2] σ_a^2 = variance of a = vector of random animal effects

[3] h^2 = *heritability*

Table 7 *Marginal distributions of heritabilities from the individual animal model Bayesian Integrated Nested Laplace Approximation analyses of binary udder traits of 740 ewes*

Trait	Parameter	Mean	SD	Percentiles			MAP
				2.5%	50%	97.5%	
Chronic mastitis (intramammary masses)	σ_a^2 [1]	0.33	0.22	0.03	0.29	0.85	0.18
	h^2 [2]	0.09	0.05	0.01	0.08	0.2	0.06
Left teat lesion	σ_a^2	0.41	0.3	0.03	0.33	1.07	0.12
	h^2	0.10	0.07	0.01	0.09	0.25	0.04
Right teat lesion	σ_a^2	0.44	0.34	0.03	0.36	1.31	0.16
	h^2	0.11	0.07	0.01	0.10	0.28	0.06
Any teat lesion	σ_a^2	0.33	0.24	0.02	0.27	0.88	0.11
	h^2	0.09	0.06	0.01	0.07	0.21	0.04

MAP = maximum a posteriori probability

[1] σ_a^2 = variance of a = vector of random animal effects

[2] h^2 = *heritability*

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Heritability of phenotypic udder traits to improve resilience to mastitis in Texel ewes

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Table S1 *Deviance information criteria (DIC) for individual animal models for ewe heritability of udder phenotypes with various combinations of fixed effects*

Phenotype	Fixed effects tested for inclusion in the model			
	FSD	FSD, EA	FSD, DIM	FSD, EA, DIM
Teat placement	2022.61	2019.92	2022.49	2019.37
Udder drop	1718.41	1708.25	1719.69	1708.94
Degree of separation	2290.07	2291.51	2291.11	2292.41
Udder width	2907.05	2894.59	2899.37	2884.11
Left teat length	725.71	725.93	719.12	722.22
Chronic mastitis	902.48	904.66	904.3	906.46
Left teat lesion	531.3	533.24	531.97	533.87
Right teat lesion	572.57	573.2	574.07	574.71
Any teat lesion	699.28	702.33	701.04	704.08

FSD = Flock observation date, EA = ewe age, DIM = days in milk. The lowest value of DIC for each phenotype was included in the model.

Table S2 *Marginal posterior distributions of variance components, heritabilities and repeatabilities of continuous traits for heritability of ewe udder phenotypic traits estimated with an individual animal model with repeated records*

Trait	Parameter	Mean	SD	Percentiles			Mode
				2.5%	50%	97.5%	
Teat placement	σ_e^2 [1]	0.634	0.0634	0.518	0.632	0.76	0.628
	σ_a^2 [2]	0.422	0.0819	0.276	0.418	0.588	0.411
	σ_{pe}^2 [3]	0.0003	0.0015	0	0.0001	0.0017	0
	h^2 [4]	0.401	0.0369	0.33	0.401	0.474	0.401
	r [5]	0.401	0.0369	0.33	0.401	0.475	0.402
Udder drop	σ_e^2	0.307	0.0415	0.23	0.305	0.387	0.298
	σ_a^2	0.156	0.0532	0.0664	0.153	0.267	0.15
	σ_{pe}^2	0.166	0.0544	0.0798	0.162	0.275	0.151
	h^2	0.244	0.0439	0.162	0.243	0.597	0.517
	r	0.517	0.0418	0.434	0.518	0.597	0.517
Degree of separation	σ_e^2	1.04	0.12	0.81	1.04	1.27	1.04
	σ_a^2	0.526	0.15	0.251	0.519	0.828	0.503
	σ_{pe}^2	0.201	0.141	0.0461	0.16	0.526	0.0447
	h^2	0.272	0.0443	0.189	0.27	0.362	0.268
	r	0.42	0.0465	0.329	0.42	0.51	0.424
Udder width	σ_e^2	2.32	0.211	1.88	2.33	2.69	2.36
	σ_a^2	0.422	0.179	0.144	0.397	0.823	0.278
	σ_{pe}^2	0.187	0.194	0.0295	0.0968	0.698	0.0294
	h^2	0.129	0.0394	0.0621	0.126	0.214	0.115
	r	0.234	0.0494	0.141	0.232	0.334	0.239
Left teat length	σ_e^2	0.0992	0.0111	0.0793	0.0988	0.121	0.098
	σ_a^2	0.085	0.0153	0.0577	0.0843	0.116	0.0833
	σ_{pe}^2	0.0002	0.0005	0	0.0001	0.0015	0
	h^2	0.462	0.036	0.391	0.462	0.533	0.472
	r	0.463	0.036	0.392	0.533	0.472	0.463

[1] σ_e^2 = variance of e = vector of random residual effects

[2] σ_a^2 = variance of a = vector of random animal effects

[3] σ_{pe}^2 = variance of u = vector of random permanent environmental effects associated with ewes

[4] h^2 = *heritability*

[5] r = ?

Table S3 *Marginal posterior distributions of variance components, heritabilities and repeatabilities of binary traits for udder phenotypes in ewes estimated with an individual animal model with repeated records*

Trait	Parameter	Mean	SD	Percentiles			Mode
				2.50%	50%	97.50%	
Chronic mastitis	σ^2_a [1]	0.36278	0.23669	0.04078	0.31901	0.92031	0.21607
	σ^2_{pe} [2]	0.0005	0.00242	0.00001	0.00007	0.00174	0.00002
	h^2 [3]	0.09666	0.05219	0.02226	0.0884	0.21917	0.05832
	r [4]	0.09671	0.05219	0.0223	0.08844	0.21919	0.05925
Left teat Lesion	σ^2_a	0.48234	0.35379	0.04008	0.40653	1.39118	0.19756
	σ^2_{pe}	0.00038	0.00165	0.00001	0.00007	0.00166	0.00002
	h^2	0.12342	0.07273	0.023	0.11073	0.29431	0.06695
	r	0.12346	0.07273	0.02306	0.11076	0.29435	0.06692
Right teat Lesion	σ^2_a	0.56167	0.3806	0.0598	0.4863	1.48308	0.33203
	σ^2_{pe}	0.00035	0.00152	0.00001	0.00007	0.00162	0.00002
	h^2	0.14128	0.07426	0.03278	0.1304	0.31263	0.10039
	r	0.14132	0.07425	0.03283	0.13045	0.31267	0.10042
Any teat lesion	σ^2_a	0.37653	0.26795	0.03245	0.32027	1.06284	0.16672
	σ^2_{pe}	0.00044	0.00203	0.00001	0.00007	0.00167	0.00002
	h^2	0.09919	0.05885	0.01841	0.08897	0.23909	0.05199
	r	0.09923	0.05884	0.01846	0.089	0.23918	0.06561

[1] σ^2_a = variance of a = vector of random animal effects

[2] σ^2_{pe} = variance of u = vector of random permanent environmental effects associated with ewes

[3] h^2 = *heritability*

[4] r = ?

Table S4 *Marginal distributions of variance components and heritabilities from an individual animal model INLA analyses of continuous udder traits in ewes with a fixed effect of litter size either included or excluded from the model*

Trait	Litter size in	Parameter	Mean	SD	Percentiles			Mode
					2.50%	50%	97.50%	
Teat placement	Yes	σ_e^2 [1]	0.714	0.078	0.571	0.712	0.868	0.71
		σ_a^2 [2]	0.302	0.089	0.15	0.296	0.487	0.284
		h^2 [3]	0.303	0.042	0.223	0.302	0.387	0.303
	No	σ_e^2	0.713	0.078	0.571	0.711	0.867	0.71
		σ_a^2	0.302	0.089	0.15	0.296	0.486	0.284
		h^2	0.303	0.042	0.224	0.303	0.387	0.299
Udder drop	Yes	σ_e^2	0.494	0.048	0.403	0.494	0.586	0.497
		σ_a^2	0.108	0.051	0.029	0.102	0.218	0.084
		h^2	0.187	0.044	0.108	0.185	0.278	0.189
	No	σ_e^2	0.496	0.05	0.403	0.496	0.591	0.499
		σ_a^2	0.122	0.053	0.039	0.117	0.237	0.1
		h^2	0.206	0.044	0.126	0.204	0.297	0.199
Degree of separation	Yes	σ_e^2	1.292	0.15	1.02	1.29	1.583	1.295
		σ_a^2	0.504	0.171	0.228	0.49	0.862	0.454
		h^2	0.288	0.044	0.205	0.288	0.377	0.284
	No	σ_e^2	1.285	0.15	1.014	1.283	1.575	1.286
		σ_a^2	0.513	0.171	0.235	0.499	0.87	0.465
		h^2	0.293	0.044	0.209	0.292	0.381	0.294
Udder width	Yes	σ_e^2	2.533	0.193	2.152	2.535	2.91	2.544
		σ_a^2	0.323	0.172	0.085	0.292	0.732	0.213
		h^2	0.106	0.038	0.043	0.103	0.191	0.097
	No	σ_e^2	2.583	0.204	2.187	2.584	2.982	2.594
		σ_a^2	0.368	0.189	0.094	0.336	0.81	0.26
		h^2	0.116	0.039	0.051	0.113	0.203	0.106
Left teat length	Yes	σ_e^2	0.111	0.014	0.085	0.111	0.139	0.111
		σ_a^2	0.076	0.018	0.046	0.075	0.113	0.072
		h^2	0.405	0.04	0.328	0.405	0.484	0.405
	No	σ_e^2	0.11	0.014	0.084	0.11	0.138	0.11
		σ_a^2	0.08	0.018	0.049	0.079	0.117	0.077
		h^2	0.421	0.039	0.344	0.421	0.498	0.423

INLA = Integrated Nested Laplace Approximation

[1] σ_e^2 = variance of e = vector of random residual effects

[2] σ_a^2 = variance of a = vector of random animal effects

[3] h^2 = *heritability*

Table S5 *Marginal distributions of sire and additive genetic variances and heritabilities from the sire model INLA analyses of binomial udder traits in ewes with a fixed effect of litter size either included or excluded from the model*

Trait	Litter size included	Parameter	Mean	SD	Percentiles			Mode
					2.50%	50%	97.50%	
Chronic mastitis	Yes	σ_s^2 [1]	0.158	0.109	0.015	0.136	0.428	0.09
		σ_a^2 [2]	0.632	0.435	0.061	0.544	1.712	0.359
		h^2 [3]	0.18	0.117	0.019	0.159	0.46	0.113
	No	σ_s^2	0.148	0.105	0.013	0.126	0.416	0.079
		σ_a^2	0.593	0.42	0.054	0.504	1.664	0.315
		h^2	0.169	0.113	0.016	0.148	0.449	0.1
Left teat lesion	Yes	σ_s^2	0.114	0.075	0.007	0.102	0.267	0.03
		σ_a^2	0.454	0.3	0.03	0.407	1.067	0.121
		h^2	0.132	0.084	0.009	0.12	0.3	0.038
	No	σ_s^2	0.114	0.075	0.008	0.105	0.265	0.031
		σ_a^2	0.458	0.298	0.03	0.418	1.059	0.123
		h^2	0.133	0.084	0.009	0.123	0.298	0.04
Right teat lesion	Yes	σ_s^2	0.221	0.165	0.016	0.182	0.636	0.098
		σ_a^2	0.882	0.66	0.065	0.728	2.543	0.392
		h^2	0.243	0.168	0.02	0.21	0.648	0.127
	No	σ_s^2	0.229	0.17	0.018	0.191	0.661	0.108
		σ_a^2	0.918	0.679	0.071	0.764	2.645	0.432
		h^2	0.253	0.171	0.022	0.22	0.669	0.139
Any teat lesion	Yes	σ_s^2	0.113	0.075	0.007	0.1	0.266	0.03
		σ_a^2	0.452	0.3	0.03	0.401	1.065	0.12
		h^2	0.131	0.084	0.009	0.118	0.299	0.038
	No	σ_s^2	0.13	0.086	0.008	0.114	0.304	0.034
		σ_a^2	0.514	0.345	0.034	0.455	1.216	0.138
		h^2	0.149	0.096	0.01	0.134	0.338	0.044

INLA = Integrated Nested Laplace Approximation

[1] σ_s^2 = variance of s = vector of random sire effects

[2] σ_a^2 = variance of a = vector of random animal effects

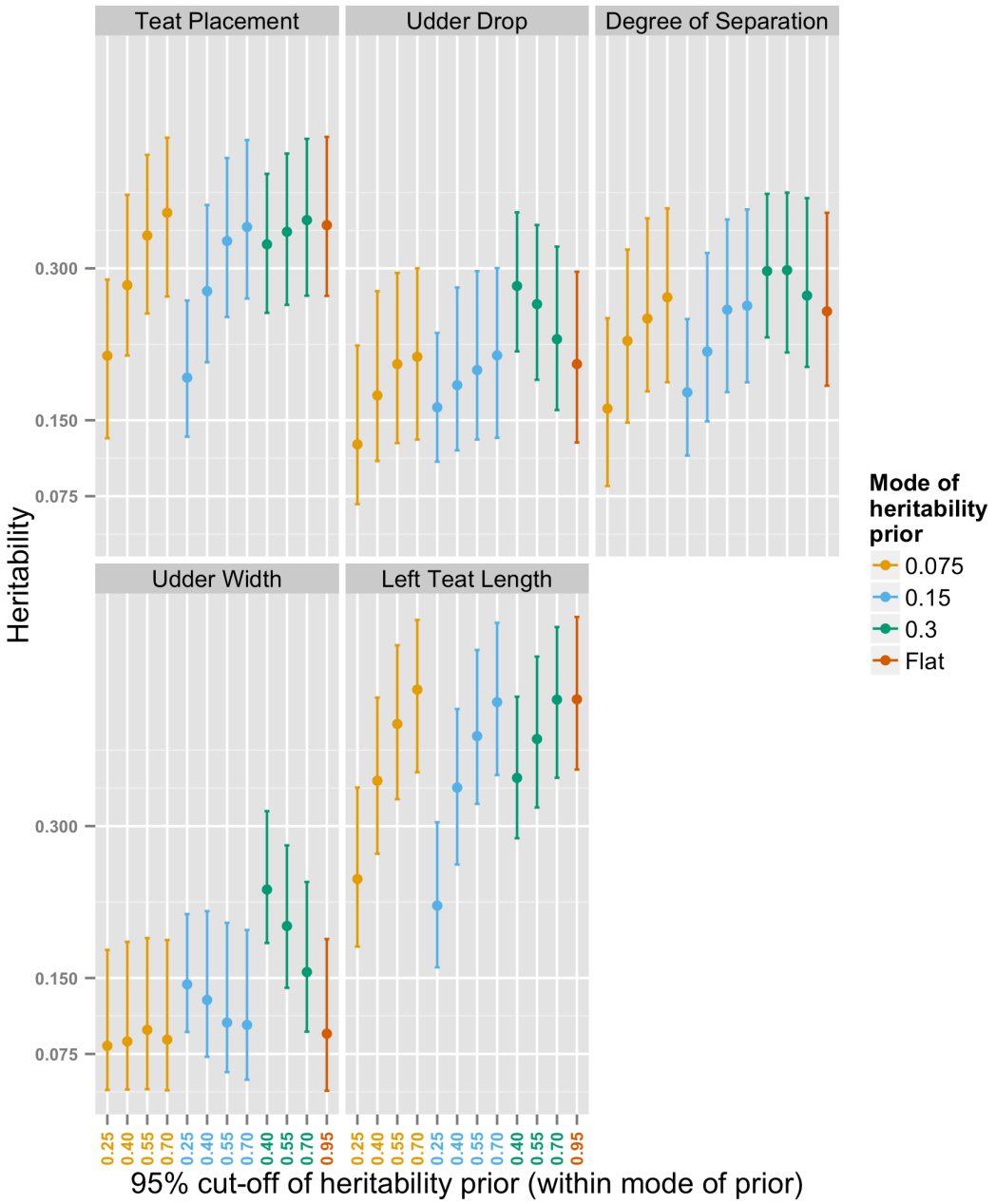
[3] h^2 = *heritability*

Table S6 *Correlations between maximum a posteriori estimated breeding value udder traits of sires with more than 5 ewe offspring*

	1	2	3	4	5	6	7	8
2. Udder drop	0.24							
3. Degree of separation	-0.29	-0.13						
4. Udder width	-0.21	-0.57	0.31					
5. Left teat length	0.09	-0.26	0.00	0.20				
6. Udder coded	-0.18	-0.08	-0.25	-0.06	0.22			
7. Left teat coded	-0.09	-0.12	-0.12	-0.16	0.01	-0.04		
8. Right teat coded	-0.17	-0.16	-0.05	0.07	-0.10	0.17	0.44	
9. Teats coded	-0.13	-0.13	-0.10	-0.01	-0.18	-0.04	0.69	0.86

1 = Teat placement

Supplementary Figure S1 *Mode and 95% confidence interval of posterior marginal distribution of heritability of continuous traits of udder morphology in Texel sheep as the mode and informativeness of the prior distribution of heritability varies*



Supplementary Figure S2 *Mode and 95% confidence interval of posterior marginal distribution of heritability of binary phenotypic udder traits in Texel ewes as the mode and informativeness of the prior distribution of heritability varies*